

Nutritional Condition of Spot Larvae Associated with the Mississippi River Plume

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Abstract.—We examined morphological criteria to determine nutritional condition, assessed recent feeding activity by examining gut fullness, and examined recent growth patterns from otoliths to determine if the Mississippi River plume front enhances feeding opportunities for larvae of spot *Leiostomus xanthurus*. A greater percentage (35%) of starved larvae, as determined by morphological criteria, occurred at the plume front than well inside (19%) or well outside (15%) the plume. Considerable variability in the incidence of starvation occurred within and between stations, especially at the plume front. The majority of spot larvae, regardless of capture location, had only a small volume ($<0.050\text{ mm}^3$) of food in their guts. The proportion of larvae that had 0.050 mm^3 or more food in their guts was equal at the plume front, well inside, or well outside the front. A low correlation ($r = -0.56$) between food volume and percent starvation, although statistically significant ($P < 0.05$), may be explained by the high variation in both variables and the different time scales of each. Gut fullness is a measure of feeding success on a scale of hours, whereas nutritional condition is a measure on a scale of days. There was minimal association between instantaneous growth rates, gut content volumes, and the degree of starvation. Larvae that exhibited the highest recent growth rate (last 3 d of life) were considerably larger for any given age than those with low rates. Our inability to demonstrate consistently that larvae have a nutritional advantage when associated with the Mississippi River plume may reflect the transitory and dynamic nature of the plume front.

The Mississippi River plume is a persistent, readily detectable feature along whose horizontal and vertical fronts zooplankton and larval fish appear to aggregate (Dagg et al. 1988; Govoni et al. 1989). The plume is a thin, buoyant lens of low-salinity, turbid water that is discharged mainly from Southwest, South, and A Loutre passes and overlies seawater of the northern Gulf of Mexico. In general, this type of plume is constrained as a thinning sheet by interfacial friction that results in the formation of a distinct frontal boundary. Observational evidence of the mixing dynamics of riverine plumes, in general, suggests that the low-salinity surface water mixes vertically with underlying seawater (Bowman and Iverson 1978). A more detailed description of the Mississippi River plume, especially during the period this study was undertaken, was given by Govoni et al. (1989).

In this study, we attempted to determine if the Mississippi River plume front enhances the nutritional condition of marine fish larvae, hence their growth and survival. Our objectives were (1) to examine morphological criteria to assess the nutritional condition of larval spot *Leiostomus xanthurus*, (2) to assess recent feeding activity by measuring the volume of food in their guts, and (3) to determine recent rates of growth from otoliths.

We chose spot because of their sensitivity to starvation and because morphological criteria to determine their nutritional condition had already been established in the laboratory (Powell and Chester 1985). Spot larvae also respond to increased food availability with increased growth that is detectable on their otoliths (Govoni et al. 1985). In addition, the reproductive and early life history of spot is typical of many marine fishes in the south Atlantic Bight and Gulf of Mexico. Spot spawn in coastal waters during the late fall and winter. The eggs are relatively small and develop rapidly. Newly hatched larvae have unpigmented eyes and lack a functional mouth and gut, and larvae in the preflexion stage are sensitive to starvation. For example, at 20°C , preflexion spot larvae must obtain food within 3 d or irreversible starvation will occur (Powell and Chester 1985). Young larvae are transported shoreward and enter estuaries that serve as nursery areas (Weinstein 1979; Warlen and Chester 1985).

Methods

Collection of material.—Spot larvae were collected from the Gulf of Mexico during cruises 131 (December 1982) and 139 (November 1983) of the National Oceanic and Atmospheric Administration (NOAA) ship *Oregon II* inside, along,

TABLE 1.—Locations of sample stations in relation to the Mississippi River plume and types of net casts for MOCNESS collections of larval spot, December 1982 and November 1983 (Govoni et al. 1989).

Cruise-station	Cast type	Location	Date	Time (hours)
131-1	Stepped oblique	5.5 km outside	5 Dec 1982	1020
131-2	Stepped oblique	7.0 km inside	5 Dec 1982	1630
131-5	Surface	Plume front	6 Dec 1982	1430
131-7	Stepped oblique	64.6 km outside	7 Dec 1982	1115
131-9	Stepped oblique	5.7 km inside	8 Dec 1982	1000
131-10	Surface	Plume front	8 Dec 1982	1230
131-12	Stepped oblique	48.7 km outside	9 Dec 1982	1000
131-16	Surface	Plume front	10 Dec 1982	0830
131-25	Stepped oblique	97.1 km outside	15 Dec 1982	1000
139-4	Stepped oblique	Plume front	24 Nov 1983	1130
139-5	Stepped oblique	Plume front	24 Nov 1983	1300
139-10	Surface	Plume front	25 Nov 1983	1455
139-13	Surface	Plume front	26 Nov 1983	1400

and outside the Mississippi River plume (Table 1). Larvae were collected with a multiple opening/closing net and environmental sensing system (MOCNESS) (Wiebe et al. 1976). The MOCNESS consisted of nine 1-m², 505- μ m-mesh plankton nets and was fished either at the surface or in stepped oblique fashion. Surface tows were taken 1 m below the surface. Stepped oblique tows were taken at discrete depths. A detailed account of our towing methods in waters in and near the Mississippi River plume was given by Govoni et al. (1989).

Spot used for morphometric measurements and stomach fullness analysis were preserved in 5% sodium borate buffered formalin. Those used for otolith analysis were preserved in 70% ethanol. Samples from nets 1, 3, 5, 7, and 9 were used for morphometric and stomach fullness analyses; those from nets 2, 4, 6, and 8 were used for otolith analysis.

Morphometric analysis.—We chose a set of morphological measurements to determine the nutritional condition of sea-caught spot larvae. Six body measurements (to nearest 0.1 mm) were made: standard length (SL), head length (HL), eye diameter (ED), body depth at the cleithral symphysis (BDC), body depth at anus (BDA), and body depth at pectoral fin base (BDP). These morphological measurements had been used previously to develop multivariate functions that accurately categorized the nutritional condition of laboratory-reared spot larvae (Powell and Chester 1985). After adjustment for differential shrinkage of sea-caught and laboratory-reared larvae (see below), measurements of sea-caught larvae were applied to the multivariate functions that were developed from laboratory-reared larvae. We used only preflexion larvae (≤ 3.8 mm SL), because they are

more sensitive to food deprivation than are older larvae (Powell and Chester 1985). Preflexion larvae also are less influenced by laboratory conditions than larger laboratory-reared spot larvae, which tend to be more morphologically robust than sea-caught larvae.

Shrinkage calibration experiments.—The multivariate functions used to assess nutritional condition were determined from measurements of preserved, laboratory-reared larvae of known nutritional condition, as reported by Powell and Chester (1985). To apply these functions to sea-caught larvae, two sets of shrinkage experiments had to be conducted. The first was to determine the effects of handling time on the body measurements of sea-caught larvae. We defined handling time as the interval between death (which we assumed occurred immediately after capture in the net) and preservation. This allowed us to convert measurements of sea-caught larvae to measurements of live, laboratory-reared larvae. The second set of experiments was to determine the effect of preservation on body measurements. This allowed us to convert measurements of live laboratory-reared larvae to measurements of preserved laboratory-reared larvae that were equivalent to the measurements from which the multivariate functions had been derived (Powell and Chester 1985).

To determine effects of handling time, laboratory-reared larvae of three stages (Table 2) were measured alive while anesthetized in tricaine and then killed in a stronger concentration of the anesthetic. Dead larvae were transferred to seawater (about 20°C) for the treatment time and then preserved in 5% buffered formalin. They were re-measured after approximately 1 month in the preservative. An analysis of covariance, in which

TABLE 2.—Number of spot larvae, by stage, used to estimate shrinkage due to handling (0 through 120 min) and due to preservation (P) only.

Treatment time (min)	Stage		
	Preflexion	Flexion	Postflexion
0	6	0	4
5	11	2	4
10	7	3	4
20	8	2	4
30	6	5	4
60	11	3	3
120	7	2	4
P	18	5	20

handling time was the covariant, was used to test the effects of handling times on the six body measurements. To determine the size-specific effects of preservation on shrinkage, individual larvae of various sizes were measured alive and placed directly in 5% buffered formalin. They were also remeasured after approximately 1 month in the preservative. Regression analysis was used to test differences between body measurements.

In order to derive an equation to convert measurements of preserved sea-caught larvae to measurements of preserved laboratory-reared larvae, both types of measurements had to be related quantitatively to a common variable (i.e., measurements of live, laboratory-reared larvae). The body measurements we used to derive the equation were

M = body measurements of preserved laboratory-reared larvae of known nutritional condition that were used to develop multivariate functions to estimate nutritional condition (Powell and Chester 1985);

M_a = body measurements of live laboratory-reared larvae;

M_f = body measurements of preserved sea-caught larvae;

M_p = body measurements of preserved laboratory-reared larvae that were placed directly in formalin (i.e., no handling time);

M_t = body measurements of preserved laboratory-reared larvae that were subjected to varying handling times before preservation (Table 2); and

β , α , b , and a = regression coefficients.

The relationships were developed in a stepwise fashion; M_f was assumed to be equivalent to M_p , and M_p was, by definition, identical to M .

Regression coefficients that were used to con-

vert body measurements of sea-caught larvae to estimates of body measurements of live laboratory-reared larvae were obtained from least-squares regression analyses. Body measurements were derived from data from the first shrinkage experiment with the equation

$$M_a = \beta M_t + \alpha. \quad (1)$$

Similarly, regression coefficients that were used to estimate measurements of laboratory-reared, formalin-preserved larvae from laboratory-reared larvae measured alive were obtained from least-squares regression analysis of

$$M_p = bM_a + a. \quad (2)$$

The solution for M_a in equation (1) can be substituted into equation (2):

$$M_p = b(\beta M_t + \alpha) + a. \quad (3)$$

Under the assumptions noted above, M and M_f can be substituted into equation (3):

$$M = b(\beta M_f + \alpha) + a. \quad (4)$$

Using parameter estimates obtained from equations (1) and (2), we adjusted measurements of sea-caught larvae with equation (4) to approximate measurements of laboratory-reared, formalin-preserved larvae of known nutritional condition, from which the multivariate functions were derived.

Gut content and growth analysis.—Larval growth rates and gut content volumes were used in combination with the morphometric technique to assess the nutritional condition of individual larvae. Gut content volume (mm^3) was estimated by assigning simple geometric shapes to specific taxa and applying length and width measurements of food items to formulae that described these shapes (Table 3). Gut content volume was the sum of the volume of individual food items. For the gut volume analysis, we used 557 preflexion larvae randomly selected from the December 1982 cruise.

Preflexion larvae randomly chosen for the analysis of growth rates were measured to the nearest 0.1 mm SL. The largest pair of otoliths (sagittae) were teased from the surrounding tissue, cleaned in distilled water, and mounted with Flo-Texx on a glass microscope slide. Growth increments were counted and measured (to nearest 0.1 μm) with an electronic digitizer interfaced to a video monitor. Microscope magnification was at least 400 \times . The assumptions that growth increments are daily and that growth of the otolith is proportional to growth of the larva have been verified (Warlen

TABLE 3.—Geometric shapes and volumetric formulae for specific taxa that we used to calculate stomach fullness (mm^3) of larval spot. Comments indicate empirically determined values for constants. Radius = r ; height = h ; diameter = d ; semiaxes of a spheroid = a (major) and b (minor).

Taxa	Comments
Right circular cylinder: $\pi r^2 h$	
Diatoms, centric	
Dinoflagellates	$h = 3 \mu\text{m}$
Cone: $\pi r^2 h/3$	
Tintinnids	
Sphere: $\pi d^3/6$	
Pteropods	
Gastropods	
Eggs	
Prolate spheroid: $4\pi ab^2/3$	
Pelecypods	
Copepods (adults and copepodites)	
Calanoids	$a = b/0.5$
Cyclopoids	$a = b/0.5$
Harpacticoids	$a = b/0.3$
Unidentified	$a = b/0.8$
Copepod (nauplii)	
Barnacle (nauplii)	
Larvaceans	$a = 400 \mu\text{m}$, $b = 300 \mu\text{m}$

and Chester 1985). Following standard age-and-growth procedures, we used the y -intercept derived from the regression of SL on otolith radius (OR) as a correction factor in back-calculating lengths (Tesch 1971). The relationship between SL and OR was linear ($r^2 = 0.56$), and its correction factor was 2.016 mm. Individual growth (SL versus age) was predominantly exponential; hence, we determined day-specific instantaneous growth rates (G) from back-calculated lengths over a 3-d period ($t = 3$ d) according to Ricker (1975):

$$G = \frac{\log_e \text{SL}_t - \log_e \text{SL}_0}{t}$$

Otoliths from 58 larvae, which were randomly sampled from two stations (131-2, 131-5), were chosen for the growth analysis. Overall differences in growth rates among collections were tested with an analysis of variance followed by Tukey-Kramer multiple-comparison test.

Results

Shrinkage Calibrations

There was a significant difference ($P < 0.05$) in body measurements between live larvae (M_a) and preserved larvae for each handling-time treatment (M_p). Except for SL, body measurements from live

larvae (M_a) were not influenced by the absolute magnitude of treatment times. For example, body measurements (except SL) of preserved larvae killed in tricaine and placed in seawater for 5 min were not significantly different ($P > 0.05$) from those of larvae killed and placed in seawater for 60 min. Statistically significant differences in the standard length relationship (SL_a versus SL_p) with treatment time were not systematic and appeared to be due to an anomalous result for one treatment. We therefore pooled all treatment times (0–120 min) to estimate regression coefficients β and α (Table 4). There was also a significant difference ($P < 0.05$) in body measurements between live larvae (M_a) and preserved larvae that had been placed directly (killed) in formalin without handling treatment (M_p). Regression coefficients b and a were estimated from these data (Table 4).

Nutritional Condition of Sea-Caught Larvae

We were unable to demonstrate that preflexion spot larvae were in better nutritional condition when they were associated with the Mississippi River plume front. In December 1982, a higher percentage of preflexion larvae appeared to be starving at the plume front (35%) than either well within (19%) or outside (15%) the plume front (Figure 1). In this analysis, we considered surface samples only, because only surface samples were taken at the plume front in December 1982. A lesser degree of starvation was observed in November 1983 than in December 1982 for larvae collected at the plume front, especially in surface samples (Figure 2). Not enough larvae were collected in November 1983 to allow a comparison of nutritional condition between larvae inside and outside the front.

Considerable variation was observed in the nutritional condition of larvae, both within and between stations at the plume front (Figure 2). For example, at station 131-5 (December 1982), where a high mean percentage (39%) of larvae were starved, only 1 of 34 fish was starved from one sample (net 9). Similar intrastation variability was evident during 1983 (Figure 2). Although a relatively low degree of starvation was observed at station 139-5 during this cruise, a large proportion of preflexion larvae from one sample (net 7) were starved.

Stomach Fullness and Growth

We compared the nutritional condition of preflexion larvae, as determined from morphometric analysis, with gut fullness to evaluate the relation-

TABLE 4.—Regression coefficients and intercepts for two sets of analyses of the effects of handling time and preservation on body measurements of spot larvae. M_a = measurements of live larvae; M_t = measurements of preserved larvae that were subjected to handling before preservation; M_p = measurements of preserved larvae that were not subjected to handling before preservation. SL = standard length; HL = head length; ED = eye diameter; BDP = body depth at pectoral fin base; BDC = body depth at cleithral symphysis; BDA = body depth at anus.

Measurement	$M_a = \beta M_t + \alpha$				$M_p = b M_a + a$			
	<i>N</i>	β	α	r^2	<i>N</i>	<i>b</i>	<i>a</i>	r^2
SL	100	1.01489	0.63453	0.98	43	0.96036	-0.25188	0.99
HL	97	1.02858	0.09228	0.98	43	0.93480	0.01002	0.96
ED	98	0.97985	0.03374	0.98	43	0.91973	-0.00659	0.98
BDP	99	1.02802	0.01754	0.99	43	1.00873	-0.04279	0.99
BDC	99	0.99964	0.04471	0.98	43	0.97955	-0.01672	0.99
BDA	97	0.98714	0.02752	0.98	43	0.96484	0.02572	0.99

ship between the two measures. The majority of larvae, regardless of capture location, had little food in their guts (Figure 3). For comparisons between stomach contents and nutritional condition, we counted those larvae with a gut content of 0.050 mm³ or more separately from those with a gut content of less than 0.050 mm³. Although the volume criterion was arbitrary, the proportion of larvae with gut contents of 0.050 mm³ or more from one area compared with the proportion from another area should have indicated short-term feeding success.

The relationship between the percentage of larvae with gut contents of 0.050 mm³ or more and the percentage of starved larvae (Figure 4) was not

strong, but it was statistically significant ($P < 0.05$). That the relationship was not stronger may be explained by the high variation in both measures and by the difference in their time scales; gut content volume is a measure of feeding success on a scale of hours, whereas nutritional condition is a measure on a scale of days.

The percentage of preflexion larvae with stomach contents of at least 0.050 mm³ was similar regardless of where samples were taken (Figure 5). If our measure of stomach content volume is an indication of food availability, then it does not appear that the quantity of food available to preflexion larvae at the plume front was dramatically different from the quantity available well inside or outside the horizontal plume front.

Instantaneous growth rates over the last 3 d of life were significantly ($P < 0.05$) different among the four collections (Table 5). Growth rates of larvae in higher-salinity (>20‰) water below the plume (station 131-2, net 6) and those in moderate-salinity (17–20‰) plume waters (station 131-5, net 4) were significantly different ($P < 0.05$) from growth rates of larvae in lower-salinity (13–17‰) plume waters (station 131-5, net 8). The groups of larvae with the highest rates of recent growth (Table 5; station 131-5, nets 6 and 8) also were distinctly larger for any given age (Figure 6) than those groups that exhibited the lowest rate of recent growth (Table 5; station 131-5, net 4; station 131-2, net 6).

There was a weak association between instantaneous growth rates, gut content volumes, and the degree of starvation on a fine-scale basis (i.e., among collections; Table 5). The group of larvae with the lowest growth rate (Table 5; station 131-2, net 6) had a relatively low percentage of starved individuals and a high percentage of individuals with gut contents of 0.050 mm³ or more. These larvae were collected below the plume.

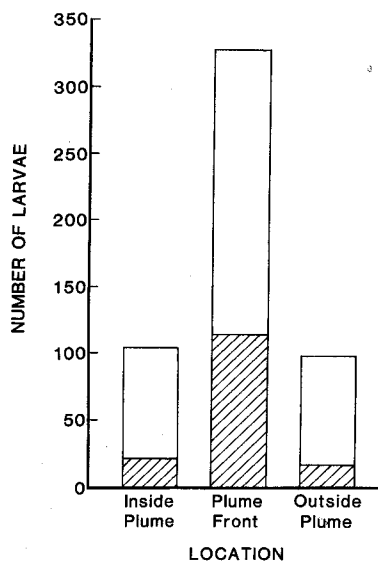


FIGURE 1.—Numbers of preflexion spot larvae collected for morphometric analysis in surface samples in or near the Mississippi River plume, December 1982. Hatched areas denote starved larvae.

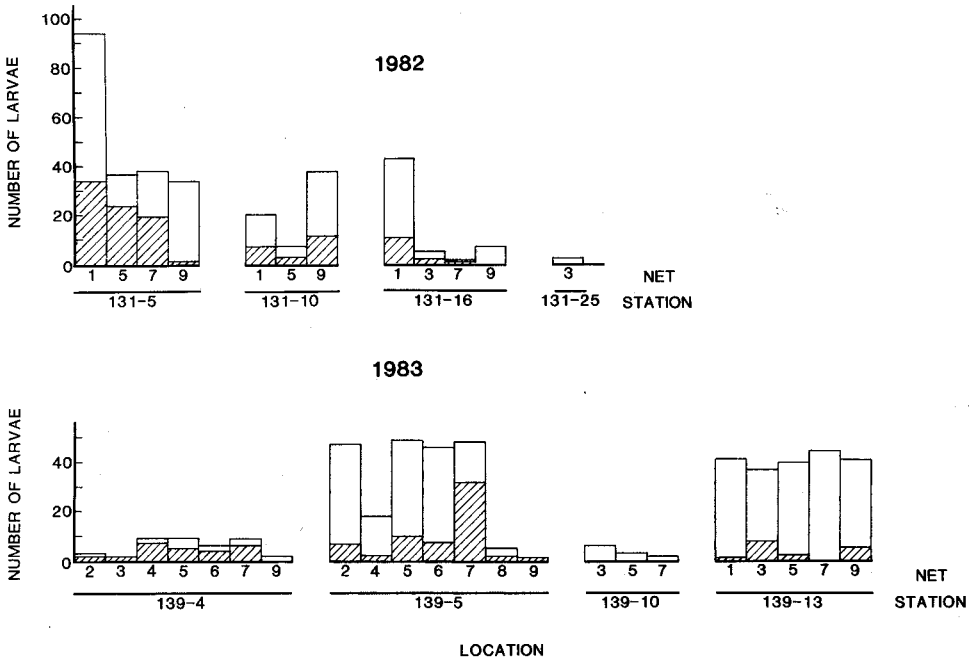


FIGURE 2.—Numbers of preflexion spot larvae collected at the Mississippi River plume front for morphometric analysis, by station and net, in December 1982 and November 1983. Hatched areas denote starved larvae.

Discussion

The use of a morphometric technique developed from an analysis of laboratory-reared fish appears to be an appropriate method to assess the nutritional condition of larvae of the same species caught in the wild. Theilacker (1986) used morphological criteria to determine the nutritional condition of sea-caught jack mackerel *Trachurus symmetricus*, compared these results with results obtained from histological criteria, and found good agreement. Although we used gut content volume and growth as other criteria for determining the nutritional status of larvae, histological criteria may be more desirable, because no shrinkage calibration is required (Theilacker 1986). Our handling time experiments differed somewhat from those of Theilacker (1986). Whereas Theilacker repeatedly measured live larvae held in a net in circulating water, we measured dead larvae that had been preserved after being held in seawater for various time periods. In our experiments, larvae held for long handling times appeared to shrink noticeably, but were largely reconstituted by preservation.

We were unable to demonstrate that preflexion spot larvae have a nutritional advantage when associated with the Mississippi River plume front.

Rather, proportionally more larvae were starved in surface waters at the plume front than well inside or outside the front. This does not accord with expectations that high primary productivity or aggregations of small food items associated with frontal areas may enhance feeding opportunities and survival of larval fishes (Richardson 1985; Dagg et al. 1988; Kiorboe et al. 1988; Govoni et al. 1989).

Variability in the nutritional condition of spot larvae within the region of the plume front may indicate the transitory and dynamic nature of this frontal area. Richardson (1985) observed that high primary production rates intermittently occurred in a permanent, but highly dynamic frontal area. Govoni et al. (1989) showed that although high densities of fish larvae occurred at the horizontal plume front, there was a high degree of variation in larval fish densities along the front both at fine (comparisons within stations) and coarse (comparisons among stations) scales. Govoni et al. (1989) also observed the convergence of flotsam along the Mississippi River horizontal plume front, which suggests that starved larvae can be carried to the frontal area from surface waters well outside or inside the front. Such water movements could have contributed to the variation in nutritional condition and feeding success we observed at the

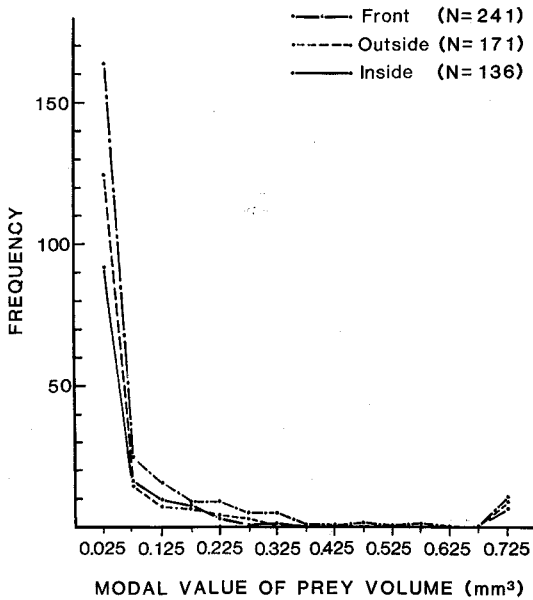


FIGURE 3.—Frequencies of gut content volumes for preflexion spot larvae collected inside, outside, and at the front of the Mississippi River plume, December 1982 and November 1983.

plume front. Dagg et al. (1988) reported on the distribution and abundance of copepod nauplii (major prey of preflexion spot larvae) at the Mississippi River plume and adjacent mixed waters. They found interannual, regional, and onshore-offshore differences in nauplii concentrations, and suggested two alternative explanations: there may be no differences between regions (i.e., stratified plume versus mixed waters well outside the plume)

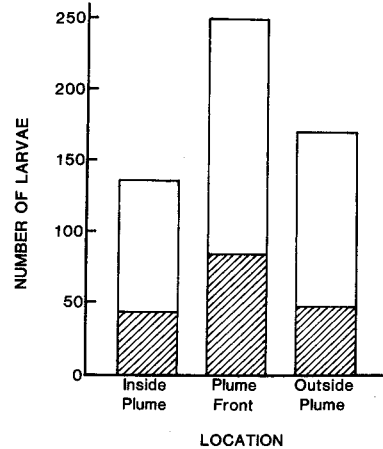


FIGURE 5.—Numbers of preflexion spot larvae randomly selected for stomach content analysis from collections in or near the Mississippi River plume, December 1982. Hatched areas denote larvae with gut content volumes of 0.050 mm³ or more.

relative to the availability of food for larval fish; or the authors failed to identify actual subregions within the Mississippi River plume environment. Dagg et al. (1988) demonstrated, however, that copepod nauplii were aggregated vertically in salinity-stratified waters, at maximum concentrations 2–10 times greater than those for nonstratified waters. They concluded that salinity-induced stratification may represent valuable habitat for larval fishes because of prey aggregation. We were unable to confirm this in our study, although Govoni et al. (1989) demonstrated that marine fish larvae occur in higher densities along the Missis-

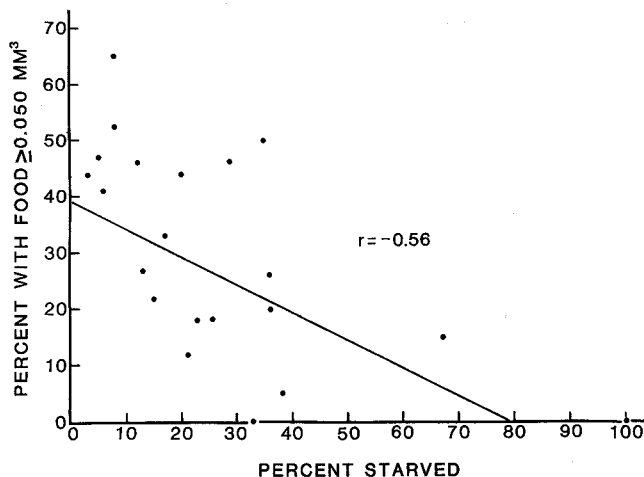


FIGURE 4.—Relationship between gut fullness (content ≥ 0.050 mm³) and starvation for samples of preflexion spot larvae.

TABLE 5.—Stations and nets sampled to obtain measures of instantaneous growth, starvation, and gut content volume for preflexion larvae of spot in or near the plume of the Mississippi River, December 1982. For instantaneous growth, N denotes the number of larvae we used for calculations. For starvation and gut content, N and % refer to the subsample of larvae that met these criteria out of the total sample.

Station	Net used for analysis of		Instantaneous growth		Starvation		Gut content $\geq 0.05 \text{ mm}^3$	
	Growth	Food and starvation	Rate	N	%	N	%	N
131-5	8	7, 9	0.0214	18	29	72	44	43
131-5	6	5, 7	0.0176	17	59	74	15	20
131-5	4	1, 5	0.0152	12	45	130	21	39
131-2	6	5, 7	0.0131	11	13	86	50	25

Mississippi River plume front than in adjacent waters. Our observation that a greater percentage of larvae were starving at the plume front than well inside or well outside the plume may be misleading. In absolute terms, more larvae actually may survive at the front than in adjacent waters because more larvae initially occur at the front. Furthermore, there could be a relatively higher abundance of food at the plume front that results in higher larval densities rather than higher growth rates.

The percentage of starvation of preflexion spot larvae observed in this study is similar to those reported for other species, but other studies have been more successful in relating the larval nutritional condition to oceanographic features. Theilacker (1986) used histological and morphological

criteria to estimate that 59% of young ($<3.5 \text{ mm SL}$) jack mackerel were starving. She related the incidence of starvation to the habitats (open ocean, islands, and banks) where larvae were collected and found that all first-feeding larvae that were collected near banks and islands were healthy. On the other hand, 45% of the first-feeding larvae that were collected in the open ocean were starving. O'Connell (1980) used histological methods to demonstrate that larvae of starved northern anchovy *Engraulis mordax* occurred in localized patches and that 60% of the larvae were starved in those samples that exhibited a high incidence of emaciation. O'Connell (1980) further observed that water with low plankton concentrations and patches of starved larvae was replaced by water with greater plankton abundance and more healthy larvae.

There appear to be discernible biological patterns associated with frontal areas, despite the high degree of variability and the dynamic physical nature of fronts (e.g., Kahru et al. 1984; Richardson 1985; Dagg et al. 1988; Kiorboe et al. 1988; Govoni et al. 1989). High, but intermittent, chlorophyll concentrations, high primary production and copepod egg production rates, and high copepod nauplii concentrations are associated with fronts and adjacent vertically stratified waters. Larval fish densities are higher in fronts, but dramatic differences in growth and nutritional condition have yet to be demonstrated.

Acknowledgments

Special thanks are extended to P. Ortner and S. Cummings (NOAA, Atlantic Oceanographic and Meteorological Laboratory) and the crew of the *Oregon II* for collection of fish larvae. Sincere appreciation is extended to C. Lewis, who made the morphological measurements, and to M. Boyd, who prepared and read the otoliths; D. Ahrenholz and R. Ferguson provided a careful review of the

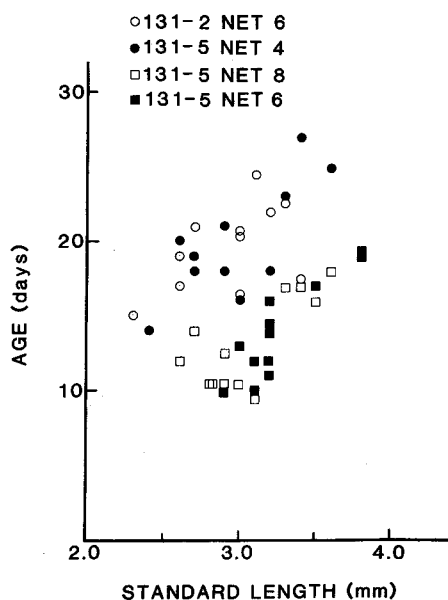


FIGURE 6.—Relationships between age and length at capture for preflexion spot larvae from four collections, December 1982.

manuscript. This research was supported in part by a contract from Ocean Assessments Division, National Ocean Service, NOAA.

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Received October 18, 1989

Accepted April 13, 1990